MIOCENE DRAGONS FROM RIVERSLEIGH : NEW DATA ON THE HISTORY OF THE FAMILY AGAMIDAE (REPTILIA: SQUAMATA) IN AUSTRALIA

J. COVACEVICH, P. COUPER, R.E. MOLNAR, G. WITTEN AND W. YOUNG

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Physignathus sp. and *Sulcatidens quadratus* gen. et. sp. nov. have been identified from a series of some 30 agamid jaw fragments recovered from the Riversleigh fossil beds. One specimen (dentary QM F18004) has a healed fracture.
The presence of *Physignathus* confirms a strong Asian influence in the composition of the Australian lepidosaur fauna as early as the Miocene. It also suggests that the Riversleigh area was well-watered at that time. Of the eight Australian Miocene lepidosaur genera, six survive. *Sulcatidens* and *Montypythonoides* are extinct.
Examination of the type specimens of the extant *Physignathus cocincinus* of Southeast Asia confirms that the Australia- ?Papua New Guinean *P. lesueurii* is properly assigned to the genus *Physignathus*. ☐ *Sulcatidens, Physignathus, Riversleigh, Agamidae, Miocene.*

J. Covacevich, P. Couper, R. Molnar, Queensland Museum, PO Box 300, South Brisbane, Queensland 4101; G. Witten, Phillip Institute of Technology, Bundoora, Victoria 3083; W. Young, Department of Oral Biology, University of Queensland, St Lucia, Queensland 4067; 21 January, 1990.

Fossils from freshwater limestones of Riversleigh Station, northwestern Queensland (c.19°02'S,138°45'E) were first reported near the turn of the century, but no serious work on them was undertaken until the 1960s. Intensive collection of this deposit began in the late 1970s with team work led by Dr Michael Archer (of the University of New South Wales; Archer, Hand and Godthelp, 1986). What is known of the Riversleigh stratigraphy and palaeoecology is summarized by Archer, Godthelp, Hand and Megirian (1989).

The rich fossil fauna includes fish, frog, reptile (crocodile, turtle, lizard, python), bird, marsupial (bandicoot, dasyurid, potoroid, phalangerid) and placental (bat, rodent) remains (Flannery, Archer and Plane, 1983; Hand, 1982, 1985). Studies of the fauna continue in many groups, including arthropods and snakes (typhlopids, elapids). Reviews and descriptions of some of these groups have been published (e.g. Smith and Plane, 1985; Hand, 1985; Archer and Flannery, 1985; and references therein). From comparisons with other fossil faunas of known age, it has been suggested that the Riversleigh deposit yielding the material described herein is of Miocene age (Archer and Bartholomai, 1978; Archer, 1981; Godthelp, pers. comm.).

Amongst material recovered are some 30 fragments of agamid skulls. Agamids are readily distinguished in having fixed, acrodont teeth which can be differentiated into 'incisors, canines and molars' (Boulenger, 1885). Agamid dentition and other distinctive characters are ably summarized by Boulenger (1885) and Estes (1983b). Modern Australian agamid maxillae and dentaries are illustrated in Fig. 1. The Riversleigh agamid material is small sized and in delicate condition. These fragments have been compared with small samples of all but one of the extant Australian genera of agamids. Not available to us is *Cryptagama* Witten 1984. (*Cryptagama aurita*, the type and only species, most closely resembles *Ctenophorus clayi*, another small cryptic dragon (Witten, unpublished data)). The fossils have also been compared with a range of agamids from other continents, either through the literature (e.g.

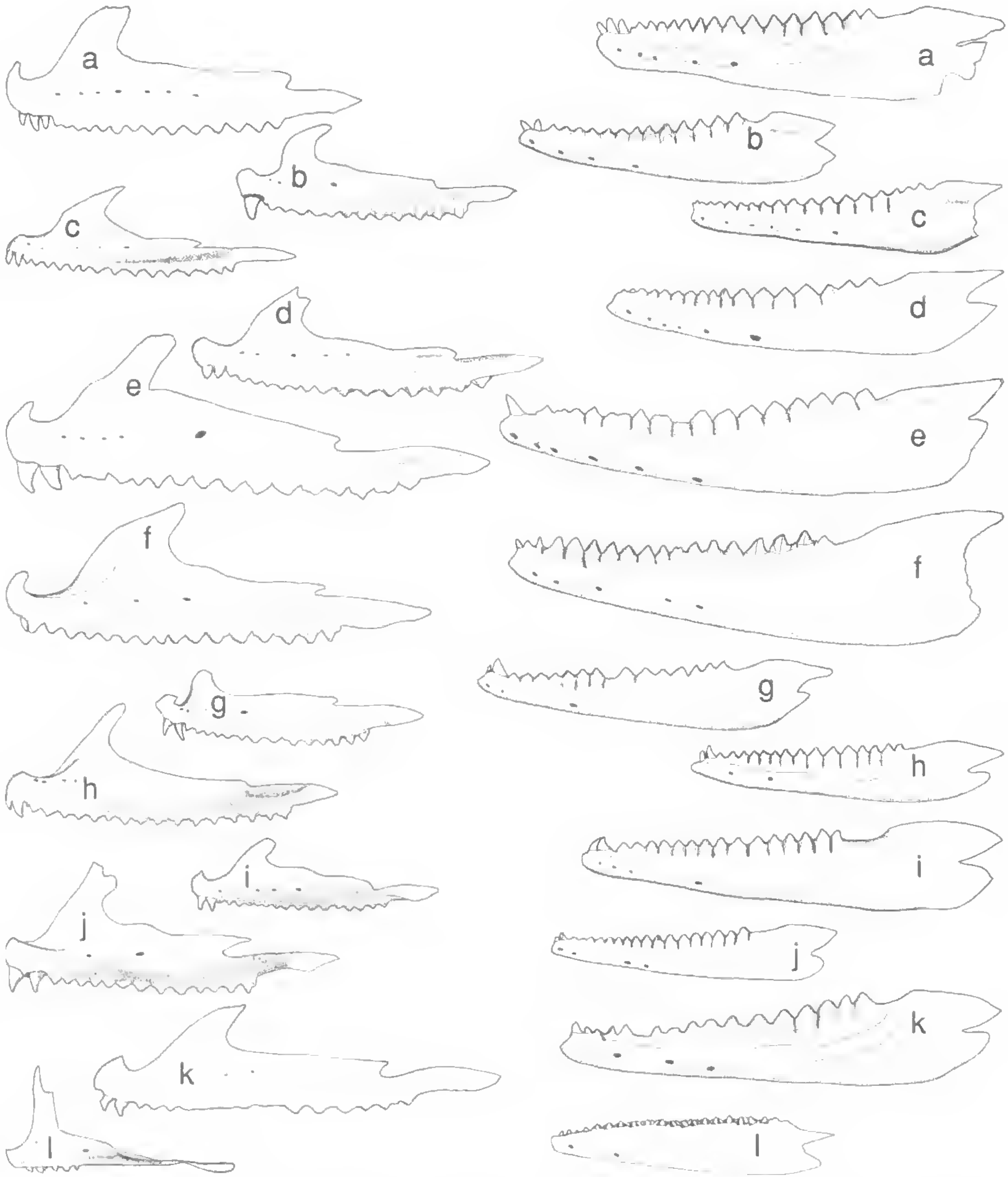


FIG. 1. Maxillae (left) and dentaries (right) from modern Australian agamids. (a) *Physignathus lesueurii* x1.5 (QM J26671); (b) *Diporiphora bilineata* x3, (QM J11141); (c) *Hypsilurus spinipes* x1.5 (QM J45306); (d) *Pogona barbata* x1.5 (QM J23950); (e) *Chamydosaurus kingii* x1.5 (QM J45307); (f) *Chelosania brunnea* x3 (WAM R41565); (g) *Caimanops amphiboluroides* x3 (WAM R15564); (h) *Tympanocryptis tetraporophora* x3 (QM J34580); (i) *Ctenophorus caudicinctus* x3 (QM J21654); (j) *Lophognathus gilberti* x1.5 (QM J39042); (k) *Gemmatophora nobbi* x3 (QM J38738); (l) *Moloch horridus* x3 (QM J11492).

Cooper and Poole, 1973; Cooper, Poole and Lawson, 1970) or with specimens (e.g. Chamaelonidae, Sphenodontidae).

Collection designations: AMNH, American Museum of Natural History, New York; MNHN, Musée Nationale d'Histoire Naturelle, Paris; QM, Queensland Museum, Brisbane, WAM, Western Australian Museum, Perth.

COMPARATIVE MATERIAL EXAMINED

Recent Australian Agamidae

Amphibolurus nobbi ♂. QM J38748, Mt Windsor Tableland, NEQ.

Caimanops amphiboluroides ♀. WAM R14464, 34km S of Warrorra, WA.

Chelosania brunnea. WAM R41565, Mitchell Plateau, WA.

Chlamydosaurus kingii. QM J3718, Zillmere, Brisbane, SEQ; QM J5707, Gulf Country; QM J19707, Rockhampton, MEQ. (dentary and maxillary fragments); QM J21929, Darwin area, NT; QM J45307, Cooktown area, NEQ; QM J47642, (juv) Wenlock, Pascoe River, Cape York, NEQ.

Ctenophorus caudicinctus ♂. QM J21654, Black Mountain, Warenda Station, WCQ.

Diporiphora bilineata ♀. QM J11141, Endeavour R., near Cooktown, NEQ.

Lophognathus gilberti ♀. QM J39042, 56.3km E of Camooweal, NWQ.

Gonocephalus boydii ♂. QM J17799, Mt Bellenden Ker, NEQ.

G. spinipes. QM J8330, Coomera Gorge, Lamington National Park, SEQ; ?, QM J45306, Richmond Range, via Bonalbo, NENSW.

Moloch horridus ♂. QM J11492, Giles, WA.

Physignathus lesueurii. QM J3865, Bellevue Station, via Coominya, SEQ; QM J5449, Brisbane, SEQ; QM J26671, Caboolture, SEQ; QM J35270, Ferguson SF, Saltwater Ck tributary, via Maryborough, SEQ. (left dentary only); QM J38108, Cobble Ck. via Samford, SEQ; QM J47339, Mt Nebo area, SEQ. (right dentary only); QM J47973, SEQ.

Pogona barbata. QM J4141, Brookstead, Darling Downs, SEQ; QM J14402, Wacol, Brisbane, SEQ; QM J23950, Everton Park, Brisbane, SEQ; QM J45852, no locality; QM J47070, Banyo, Brisbane, SEQ; QM J47077, Brisbane, SEQ.

Tympanocryptis tetraporophora ♂. QM J34580, Cuddapan Station, via Windorah, SWQ.

Recent Foreign Agamidae

Uromastyx aegypticus. AMNH 73160, Saudi Arabia; AMNH 74816, Saudi Arabia.

Physignathus cocincinus. MNHN Ag82, MNHN 2537, MNHN 1856, MNHN 2536.

Chamaeleonidae

Chameleo (?) basiliscus. QM J45322, no data.

Iguanidae

Iguana sp. QM J49263, no data.

Sphenodontidae

Sphenodon punctatus. QM J1046, New Zealand.

Fossil Agamidae

Middle to late Miocene specimens, Gag Site. QM F18031-F18033.

Early Miocene specimens, Godthelp Hills and Hal's Hill sequence. QM F18004-F18011, QM F18014-F18030.

?, Inabayance Site. QM F18012-F18013.

FOSSIL AGAMIDS FROM RIVERSLEIGH

Identification of this material has been confounded by the small size and fragility of the fragments and by the fact that they are all from only dentaries or maxillae. Not one piece of cranium has yet been found. The studies by Cooper and Poole (1973) and Cooper et al. (1970) have been very useful in regard to cranial and dental anatomy comparisons and in recognising ontogenetic changes. Despite this, however, distinguishing juveniles from adults and making identifications from only a few characters has been difficult. In the descriptions which follow, the extent of our material is shown in accompanying diagrams. The material present is shaded on stylized agamid skulls or jaws, based on those of *Diporiphora bilineata*. The descriptions concentrate on features of potential taxonomic significance.

In an effort to refine the process of identification of these small fragments, epoxy resin replicas of QM J5449, J47339 (*Physignathus lesueurii*) and of fossil specimens QM F18024, F18011, F18018 and F18015 were made for comparisons of microwear patterns. The replicas were sputter coated with gold and examined under a Phillips 505 scanning electron microscope to compare anatomical features with those produced by wear. However, there are few microwear features on the specimens and, consequently, they are of no diagnostic significance.

Family AGAMIDAE Gray, 1827
Physignathus Cuvier, 1829
Physignathus sp.

QM F18004

LOCALITY

Camel Sputum Site (Camel Sputum local fauna).

DESCRIPTION

A portion of left dentary which bears 12 acrodont teeth and a trace of the 13th acrodont tooth. Length 17.38mm, maximum depth (excluding tooth row) 3.71mm. There is a healed fracture in the mid tooth row. The fracture has healed out of alignment, displacing the anterior half of the dentary towards the labial.

The labial surface of the dentary is vertically notched between the tooth bases. Three foramina are present close to the ventral surface, below the third, fifth and seventh acrodont teeth. The anterior ventral surface of the dentary is badly weathered, so it is impossible to determine whether more foramina were present. On the lingual surface a longitudinal groove runs beneath the tooth bases. This groove shallows posteriorly. It is not continuous, having been displaced by the mid-dentary fracture. A large foramen is present in the roof of the Meckelian Groove, below the third posteriormost acrodont tooth. When viewed occlusally, the displacement of the tooth row is obvious. Both tooth surfaces are rounded, but the lingual is slightly flattened. An inward curve can be detected towards the anterior tip of the dentary.

QM F18007

LOCALITY

Camel Sputum Site (Camel Sputum local fauna).

DESCRIPTION

Right dentary; length 17.67mm; maximum depth (excluding teeth 4.96mm). No pleurodont teeth are present, although one empty 'socket' is visible in occlusal aspect. The first and third acrodont teeth are damaged.

In a labial view, only one foramen is visible, situated below the eighth acrodont tooth. The labial surface is pitted and there are deep notches at the bases of the acrodont teeth.

Viewed occlusally the acrodont teeth are rounded on both lingual and labial surfaces. The posterior three acrodont teeth are weakly cusped. The lingual faces are slightly flattened. The anterior tip of the dentary curves inward. On the lingual face of the dentary a deep groove runs below and parallel to the acrodont tooth row. The Meckelian Groove is clearly visible, but badly chipped anteriorly.

QM F18008

LOCALITY

Wayne's Wok (Wayne's Wok Site local fauna).

DESCRIPTION

Right, worn maxilla bearing 11 acrodont teeth, with a flattened labial aspect. Length 16.25mm; maximum depth (excluding teeth) 4.01mm. The posterior three acrodont teeth are weakly cusped.

On the labial surface, there is a slight inward curve of the maxilla, tilting the tooth row lingually. High on the labial face, below the posterior margin of the nasal process, are two foramina. Further foramina are present in the groove parallelling the maxillary/jugal/lacrimal suture. The largest of the foramina lies directly behind the nasal process. Posterior to this are four small foramina. A small process projecting towards the rear of the maxilla is situated posteriorly on the maxillary/jugal suture. This is located above the third acrodont tooth from the posterior margin of the tooth row. There is a broad palatal process that reaches its widest point towards the middle of the tooth row, then rapidly tapers off, becoming almost non-existent posteriorly.

QM F18012

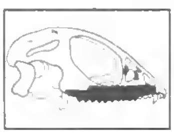
LOCALITY

Wayne's Wok (Wayne's Wok Site local fauna).

DESCRIPTION

Portion of right maxilla bearing complete acrodont tooth row. Length 19.67mm, maximum depth (excluding teeth) 3.81mm (Fig. 2).

The first four acrodont teeth are damaged, but



the rest of the acrodont tooth row has a flattened labial aspect and the teeth are slightly cusped. The acrodont teeth are moderately 'shouldered'. The maxilla has a

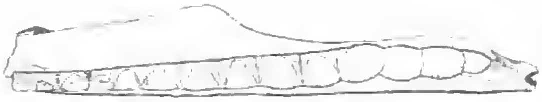


FIG. 2. Occlusal view of QM F18012 x3.

slight inward curve tilting the acrodont teeth lingually. Three foramina are present on the labial surface above the third acrodont tooth; and a further two above the sixth and eighth acrodont teeth. Three foramina are present in the groove which runs parallel to the jugal/maxilla/lacrimal suture. A small process projecting towards the rear of the maxilla is situated posteriorly on the maxillary/jugal suture. This is located above the third acrodont tooth from the posterior margin of the tooth row. On the lingual surface, the palatal process is moderately developed anteriorly, broadening to its widest point half way along the acrodont tooth row, then narrowing posteriorly.

QM F18013

LOCALITY

Inabayance Site.

DESCRIPTION

Almost complete left side of snout, including the premaxilla. Length 18.13mm; maximum depth (excluding teeth) 14.07mm. Perfect suture definition is present between the premaxilla, nasal, maxilla and prefrontal (Fig. 3). The

pleurodont teeth of the premaxilla and maxilla have not been preserved. The anterior four acrodont teeth are reduced from wear, each tooth being difficult to distinguish from those adjoining it. The posterior four acrodont teeth are intact, their broad triangular form being well preserved.

QM F18014

LOCALITY

RSO Site.

DESCRIPTION

Specimen F18014 is a fragment of the left dentary, bearing eight acrodont teeth. Length 11.24mm, maximum depth (excluding teeth) 3.66mm.

The labial surface of the dentary is deeply notched vertically between the tooth bases. Also clearly visible is a single foramen placed close

to the ventral surface of the dentary, below the third acrodont tooth. The lingual surface bears a distinct longitudinal groove immediately below the tooth row. This groove shallows posteriorly. In the roof of the Meckelian Groove is a large foramen below the fifth acrodont tooth. Occlusally viewed, both tooth surfaces are gently rounded, but slightly flattened labially.

QM F18016

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Damaged right dentary, bearing two pleurodont and eight acrodont teeth. Behind the eighth acrodont tooth the fragment is damaged, revealing two internal longitudinal cavities, one

above, and the other below, the Meckelian groove. Length 14.60mm, maximum depth (excluding teeth) 3.28mm. The labial face of the dentary bears four foramina, one below each of the pleurodont teeth and one below the second and sixth acrodont teeth. Strong vertical notch-

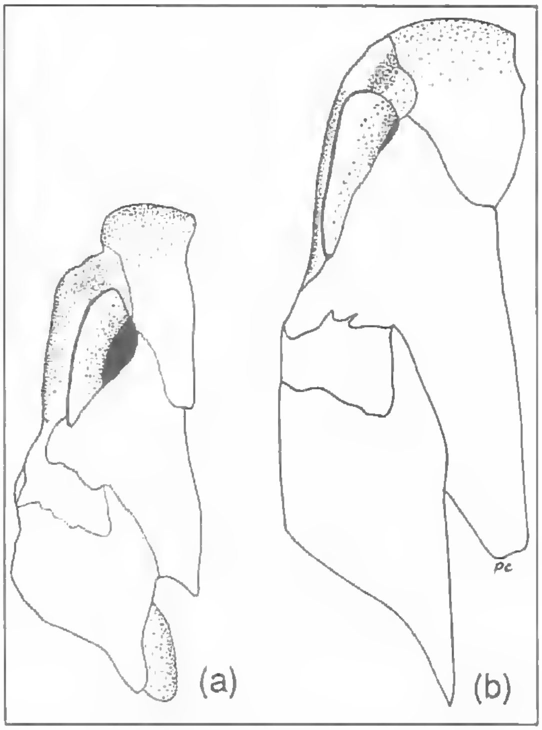


FIG. 3. Dorsal view of snout, illustrating variation in sutures between (a) *Physignathus* sp. x3 (QM F18013) and (b) *Physignathus lesueurii* x3 (QM J5449).

ing is evident at the bases of the acrodont teeth. The occlusal aspect shows a distinct inward curve of the dentary anteriorly. Both lingual and labial faces of each acrodont tooth arc rounded, the tooth margin being centrally positioned. On the lingual surface of the dentary a distinct groove runs below the tooth row. The Meckelian Groove is clearly defined and has a distinct foramen posteriorly on the upper surface.

QM F18017

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Specimen F18017 is the upper anterior portion of the left dentary. Eight acrodont teeth are present on this fragment, the first and third broken at the base. Length 9.64mm, maximum depth (excluding teeth) 2.17mm.

The labial surface exhibits deep vertical notching between the tooth bases and, on the lingual

surface, the only distinctive feature preserved is a longitudinal groove below the tooth bases. Viewed occlusally, both tooth surfaces are rounded but the labial is more strongly convex. A slight curvature of the jaw line is evident.

QM F18018

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

An almost complete left dentary with 14 acrodont teeth and three pleurodont teeth. Acrodont teeth two, three, four and seven are damaged. Length 24.38mm; depth (including tooth row) 4.76mm (Fig. 4).

Below the tooth row there is a distinct lon-

gitudinal groove lingually which shallows posteriorly.

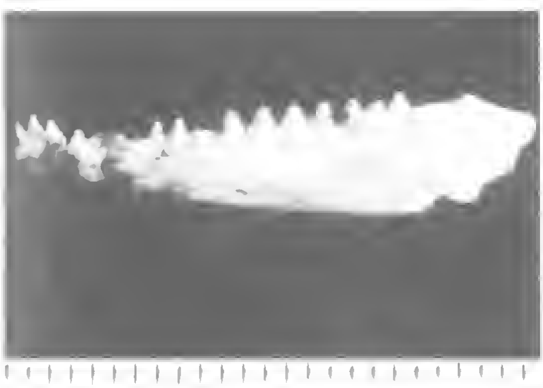


FIG. 4. *Physignathus* sp. (QM F18018).

QM F18019

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Anterior half of left dentary, bearing three forwardly inclined pleurodont teeth and eight acrodont teeth; length 12.64mm, maximum depth (excluding teeth) 2.67mm.

The second tooth is the larger. The acrodont

teeth are sharply tipped and distinctly grooved at their bases labially along most of the tooth row. There are six foramina on the labial surface; one below each of the pleurodont teeth, and one below the second, fourth and seventh acrodont teeth. When viewed occlusally the acrodont teeth are rounded both lingually and labially and the dentary has a distinct inward curve anteriorly. On the lingual surface beneath the tooth row is a distinct longitudinal groove, which shallows posteriorly.

QM F18020

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Specimen F18020 is a portion of mid to anterior right dentary, bearing eight acrodont teeth. Length 9.09mm; maximum depth (excluding teeth) 3.27mm.

The labial face of the dentary is deeply notched vertically at the tooth bases. Three foramina are present towards the ventral surface, one each below the second, third, and sixth acrodont teeth. On the lingual surface a longitudinal groove runs beneath the tooth bases. The Meckelian Groove is clearly defined. Occlusally viewed both tooth surfaces are rounded but the lingual face is less convex. Anteriorly the tooth row curves medially.

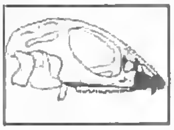
QM F18021

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Tip of right maxilla. Length 9.10mm, maximum depth (excluding teeth) 4.54mm. This fragment bears one complete acrodont tooth, followed by three damaged teeth. There are two pleurodont teeth, posteriorly inclined, and one empty socket.



A ridge is present on the labial surface of the maxilla. This originates at the base of the third pleurodont tooth and runs parallel to the acrodont tooth row. Below this ridge the maxilla is flexed lingually. Six foramina are present, three on the labial surface, one in the ventral margin of the naris and two in a groove where the maxilla joins the jugal behind the nasal process. The position of these foramina corresponds closely to those of F18024.

QM F18022

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Damaged left dentary. The anterior tip of the dentary is also damaged behind the second acrodont tooth. Two (possibly three) acrodont teeth are missing. All but the anterior six acrodont teeth are weakly cusped. Length 18.31mm; maximum depth (excluding teeth) 3.01mm (Fig. 5).

Anteriorly three pleurodont teeth, which incline slightly anteriorly, are present. Three prominent foramina are present labially, one each below both the second and third pleurodont teeth, and one below the second acrodont tooth.

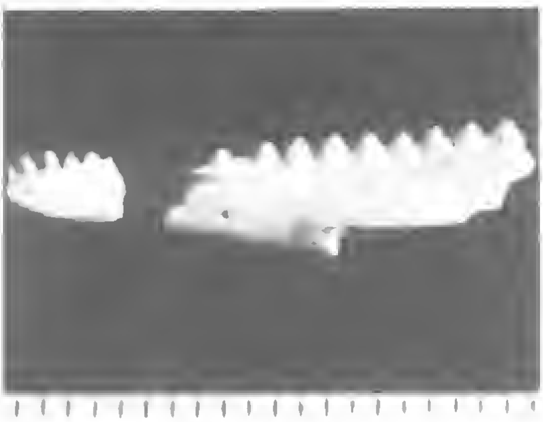


FIG. 5. *Physignathus* sp. (QM F18022).

The body of the dentary bears nine acrodont teeth, the first of which is damaged. There is a foramen below this first damaged tooth. The acrodont teeth have rounded labial and lingual surfaces, and deep vertical grooves at the bases on the labial aspect. On the lingual surface a distinct longitudinal groove runs beneath the tooth row. This groove shallows posteriorly. The Meckelian Groove is distinct and contains a foramen, situated below the fourth acrodont tooth from the posterior margin of the tooth row.

QM F18024

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Left maxilla, bearing complete tooth row. Length 18.5mm, maximum depth (excluding teeth) 5.44mm. There are 13 acrodont teeth, and two pleurodont teeth. Anterior to these is an empty 'socket' of a third pleurodont tooth.

A distinct ridge is present on the labial surface. This rises at the base of the third pleurodont tooth and runs parallel to the acrodont tooth row. Below this ridge, the maxilla inclines inwards. Five foramina are present on the labial face of the maxilla, beginning above the third pleurodont tooth and running back to the seventh acrodont tooth. Viewed from above the teeth are worn labially and rounded lingually. The acrodont teeth are weakly cusped. A distinct groove is present, running parallel to the maxillary/jugal/lacrimal suture just above the palatal process. This groove contains five foramina, two of which lie behind the nasal process. The second foramen is the largest. The remaining three are of equal size and are situated above the seventh and eighth acrodont teeth. On the lingual surface of the maxilla a distinct palatal process is present above the acrodont tooth row. This process is moderate anteriorly, broadening to its widest point half way along the acrodont tooth row. It then narrows and is only barely visible below the posterior acrodont teeth.

QM F18025

LOCALITY

Upper Site (Upper site local fauna).

DESCRIPTION

Right maxilla bearing a complete acrodont tooth row of 14 teeth and 1 pleurodont tooth.

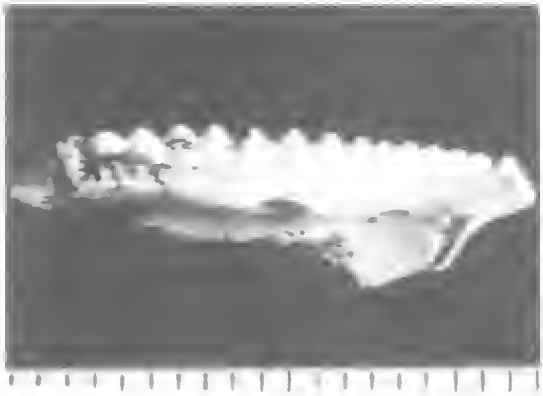
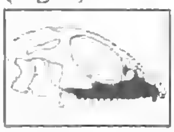


FIG. 6. *Physignathus* sp. (QM F18025).

Length 19.31mm; maximum depth (excluding teeth) 4.93mm. Just posterior to the anterior tip a ridge of enamel is preserved, indicating the presence of at least one other pleurodont tooth. The nasal process, the palatal process and the posterior tip of the maxilla are slightly damaged (Fig. 6).



Three foramina are present on the labial surface; one above the second acrodont tooth; and one each above the sixth and eighth acrodont teeth. Three additional foramina are present in the groove which parallels the jugal/maxilla/lacrimal suture; the anterior (below the nasal process) is the largest. The remaining two foramina are slightly smaller and lie above the eighth and ninth acrodont teeth. There are also four small foramina in this groove and one lies on the floor of the naris. A small process projecting towards the rear of the maxilla is situated posteriorly on the maxillary/jugal suture. This is located above the third acrodont tooth from the posterior margin of the tooth row. The rear six acrodont teeth are weakly cusped ('shouldered').

On the lingual face of the maxilla, there is a broad palatal process which reaches its widest point opposite the eighth and ninth acrodont teeth and is only barely discernable at the 11th acrodont tooth. A small secondary flange is present opposite the 13th and 14th acrodont teeth. The acrodont tooth row, occlusally viewed, has a flattened labial aspect. The pleurodont tooth is strongly inclined outwards.

QM F18026

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Portion of the right maxilla bearing eight acrodont teeth. Three of these (the posterior two and the fifth from the posterior margin) are damaged. Length 9.98mm, maximum depth (excluding teeth) 3.93mm.

The labial face of the maxilla has a distinct longitudinal ridge about halfway down. Below this ridge, the maxilla and tooth row slope inwards. Two foramina are present, the first and larger is situated above the second anterior most tooth, and above the longitudinal ridge. The second foramen is much smaller, situated above the third tooth, and below the longitudinal ridge. A further three foramina are present in the groove running parallel to the maxillary/jugal/lacrimal suture. These lie close together and are situated anteriorly. The anteriormost foramen is the smallest and the posteriormost is the largest. Viewed laterally, the acrodont teeth are 'shouldered'.

On the lingual face of the maxilla is a broad palatal process which tapers posteriorly on the tooth row. Posteriorly, near the dorsal edge of the medial surface of the labial face there is a deep notch positioned posteriorly in the groove running parallel to the maxillary/jugal suture. This notch is normally associated with the posterior process of the maxillary/jugal suture. On specimen F18026 the process has not been preserved, but the position of the groove indicates that the process was positioned anterior to the end of the tooth row.

Viewed occlusally, the teeth have a flattened labial face and the lingual surface is distinctly rounded. Posteriorly in the tooth row the teeth have a distinct wear facet on the anterior face.

QM F18027

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Left dentary bearing complete tooth row. The two anterior-most acrodont teeth are damaged and the three pleurodont teeth are represented by broken stumps. Length 18.96mm, maximum depth (excluding teeth) 3.81mm.

The labial face of the dentary bears four foramina; one below both the second and third pleurodont teeth, and one below both the second and fifth acrodont teeth. When viewed occlusally the acrodont teeth are rounded on both the lingual and labial surfaces and the dentary exhibits a distinct inward curve anteriorly. On the lingual surface beneath the tooth row is a distinct longitudinal groove which shallows posteriorly.

QM F18028

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Right dentary bearing 12 acrodont teeth; length 16.38mm, maximum depth (excluding teeth) 3.55mm. The acrodont tooth row is almost complete.

The labial surface of the dentary is pitted. Nonetheless two foramina are clearly visible below both the third and fifth anterior-most acrodont teeth. Deep notching is visible between the acrodont tooth bases, except on the two posterior acrodont teeth. On the lingual surface of the dentary, a distinct longitudinal groove shallowing posteriorly runs immediately below the tooth bases. There is a large foramen on the roof of the Meckelian Groove, below the sixth and seventh anterior-most acrodont teeth. Occlusally viewed both surfaces of the teeth are rounded, but the lingual is slightly flattened. A slight inward curve of the dentary is detectable anteriorly.

QM F18029

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Anterior fragment of left dentary bearing one pleurodont and several acrodont teeth. There are two empty 'sockets' of pleurodont teeth, one on either side of the tooth. The first two of the acrodont teeth are in good condition. Length 9.45mm; maximum depth (excluding teeth) 2.52mm.

Occusally viewed, the dentary anteriorly displays a distinct inward curve. The pleurodont tooth is slightly procumbent. Four foramina are present on the labial surface of the dentary; one below both the second and third pleurodont teeth; one below both the third and sixth acrodont teeth.

QM F18030

LOCALITY

Upper Site (Upper Site local fauna).

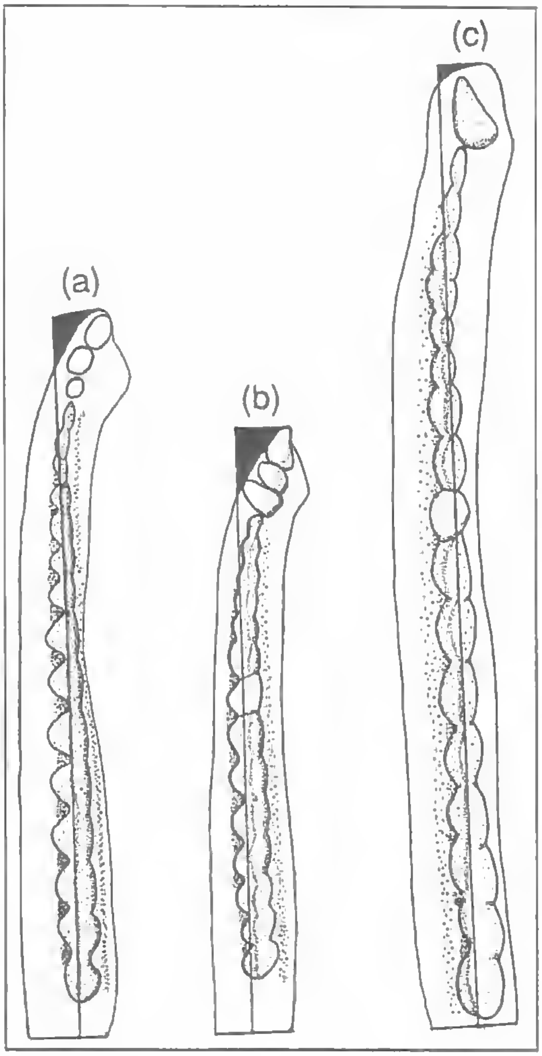


FIG. 7. Occlusal view of dentaries illustrating the varying degrees of dentary curvature between (a) *Physignathus lesueurii* x3 (QM J26671), (b) *Physignathus* sp. x3 (QM F18018) and (c) *Chlamydosaurus kingii* x3 (QM J45307).

DESCRIPTION

Fragment of right anterior maxilla bearing seven acrodont teeth. The 3rd anteriormost is damaged, broken off at the base. Length 9.54mm; maximum depth (excluding teeth) 3.15mm.

In a labial view, the lower edge of the maxilla curves inward. Four well-spaced foramina are present on the labial face, above the first, third, fifth and sixth acrodont teeth. The acrodont teeth have well rounded tips. The teeth are not cusped. Viewed occlusally, the labial tooth surface is flattened. The lingual surface is very angular, with both the anterior and posterior faces flattened, giving the teeth a three sided appearance. On the lingual face of the maxilla there is a broad palatal process. Four foramina are situated in the groove in the base of the nasal process, the anteriormost above the third acrodont tooth. The remaining three are above the fifth and sixth acrodont teeth.

IDENTIFICATION

The specimens F18004, F18007-8, F18012-14, F18016-22, F18024-30 are all referred to *Physignathus* sp. Dentary F18018 is one of the best preserved in the sample and, although the numbers of and wear pattern on agamid teeth vary greatly (Cooper and Poole, 1973), it shows similarity to the dentary of *Chlamydosaurus*, *Lophognathus*, *Amphibolurus*, *Physignathus*, *Ctenophorus*, *Pogona* and *Diporiphora*. This specimen is easily distinguished from *Chlamydosaurus kingii* by number of acrodont teeth (19-20 in *C. kingii* vs 14 in F18018); number of pleurodont teeth (1-2 vs 3); shape and size of pleurodont teeth (one very large caniniform tooth, with one smaller tooth on right ramus vs three teeth, with the first the smallest, followed by two teeth of almost equal size). Further, the upper edge of Meckel's Groove in *C. kingii* lacks the slight upward curve present in F18018, and the mid-line (occlusally viewed) of the dentary in *C. kingii* is almost straight, whilst in F18018 this curves markedly inward anteriorly. The dentaries of *Ctenophorus*, *Pogona*, *Lophognathus*, *Amphibolurus*, *Diporiphora* and *Physignathus* have the distinct medial anterior curve of specimen F18018. However, *Lophognathus*, *Amphibolurus*, *Ctenophorus* and *Pogona* specimens lack the enlarged forward projecting teeth of F18018 and *Pogona* has only two pleurodont teeth (vs three in F18018).

Specimen F18018 and the dentary QM J26671 (*Physignathus lesueurii*) are very close (Fig. 7). Table 1 summarizes these comparisons.

F18018 does not differ in any substantial degree from specimens of the extant *P. lesueurii* (Gray 1831), but, from only this dentary we cannot assign it to this species with any certainty.

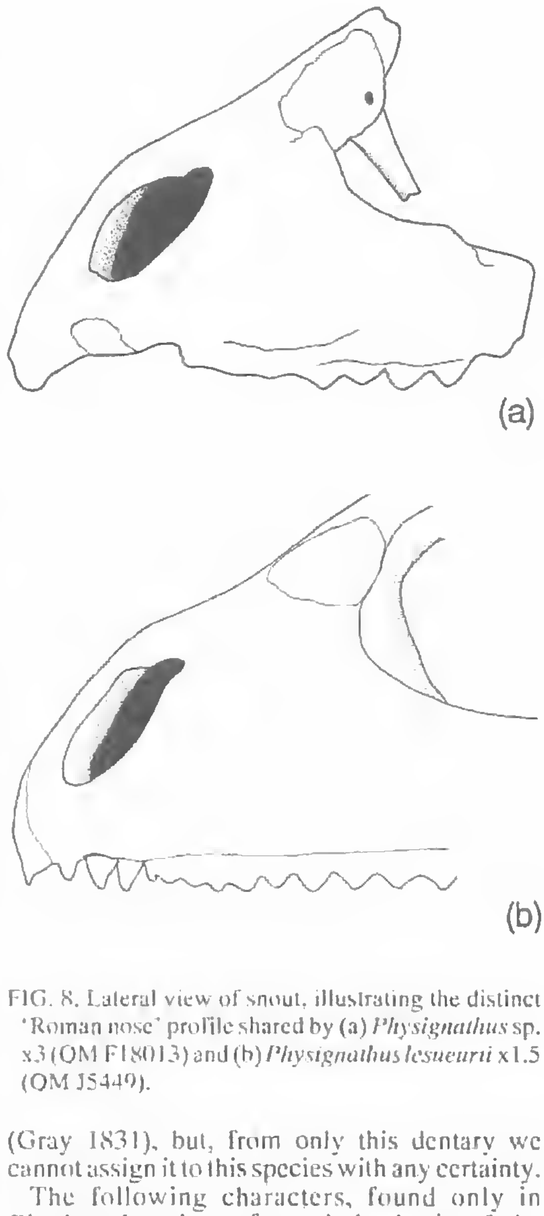


FIG. 8. Lateral view of snout, illustrating the distinct 'Roman nose' profile shared by (a) *Physignathus* sp. x3 (QM F18013) and (b) *Physignathus lesueurii* x1.5 (QM J5449).

The following characters, found only in *Physignathus*, have formed the basis of the remaining identifications: the form of the inward curve on the dentary (F18004, F18007, F18019, F18022, F18027, F18028, F18029); the lingual longitudinal groove below the bases of the dentary teeth (F18004, F18007, F18014, F18016, F18019, F18022, F18027, F18028); the number, shape, size and cusping of the acrodont dentary teeth (F18004, F18007, F18014, F18016, F18019, F18022, F18027, F18028); the number, shape, and size of the pleurodont dentary teeth (F18016[1], F18019, F18022, F18029); the degree

[1] F18016 has only two pleurodont teeth, while three are present in other complete material in the sample. Examination of modern *Physignathus* confirms that this character varies between two (QM J35270) and three (other material examined).

TABLE 1. A comparison of the dentaries of F18018 (Riversleigh fossil agamid) with J26671 (*Physignathus lesueurii*).

CHARACTER	F18018	J26671
acrodont tooth number	14	15
pleurodont tooth number	3	3
angle of projection of pleurodont teeth	1, anteriorly; 2,3 upward and anteriorly	1, anteriorly; 2,3 upward and anteriorly
curvature of midline of jaw (occlusal view)	marked	marked
pattern of tooth wear	lingual face flattened; labial face rounded	lingual face flattened; labial face rounded

of flattening of the labial aspect of the acrodont teeth (F18012, F18024, F18025, F18030); the number, shape, size and cusping of the acrodont maxillary teeth (F18008, F18012, F18025, F18026); the number, shape and size of the pleurodont teeth on the premaxilla-maxilla (F18021, F18024, F18025); proportions of the palatal process (F18008, F18012, F18024, F18025, F18026); the steeply-sloped posterior edge of the narial opening (F18012, F18024, F18025); the 'Roman-nose' profile (F18013) (Fig. 8); shape and position of the nares (F18013); the form of the small posterior maxillary process (F18008)(Fig. 9).

Family Agamidae Gray 1827
Sulcatidens gen. nov.

TYPE AND ONLY SPECIES
Sulcatidens quadratus gen. nov. and sp. nov.

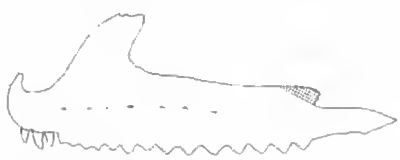


FIG. 9. Maxilla from *Physignathus lesueurii* x1.5 (QM J26671), showing the position of the posterior maxillary process. Similar processes are present in many of the modern agamid maxillae examined (Fig. 1) and in fossil maxillae where they are complete enough (e.g. F18008). This feature has not been used previously to help identify agamid fragments.

FIG. 10. Occlusal view of the holotype of *Sulcatidens quadratus* gen. et sp. nov. QM F18010 x3.

GENERIC DIAGNOSIS
Sulcatidens is distinguished from all other agamids in having the distal margins of the posterior maxillary teeth set in a notch in the mesial margin of the adjacent posterior crown.

ETYMOLOGY
From the Latin *sulcare*, to furrow, in reference to the notches or furrows in the mesial margins of the posterior maxillary teeth. The gender is masculine.

Sulcatidens quadratus sp. nov.

HOLOTYPE
QM F18010, an incomplete right maxilla bearing 11 acrodont teeth (Fig. 10).

TYPE LOCALITY
Wayne's Wok Site, Riversleigh Station, NW Queensland. Miocene.

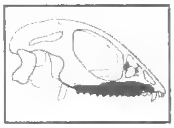
SPECIFIC DIAGNOSIS
As for the genus.

ETYMOLOGY
From the Latin *quadratus*, from *quadrare*, to

make square. Named in reference to the nearly quadrate profile of the posterior maxillary teeth.

DESCRIPTION

Right maxilla bearing 11 acrodont teeth, length 18.28mm, maximum depth (excluding teeth) 3.92mm. On the lingual face of the maxilla, some of the bases of the teeth are corroded.



In labial view the maxillary face is rounded, tilting the acrodont tooth row lingually. The acrodont teeth are cusped, and their tips are directed posteriorly. The four posteriormost acrodont teeth are unusual, distinct from the typical triangular agamid dentition. In profile, these teeth are almost quadrate and are very closely spaced. Viewed occlusally the acrodont teeth are flattened on the labial face. The four posterior acrodont teeth are very distinct in form from those situated more anteriorly in the toothrow. In most agamids the posterior acrodont teeth slightly overlap, as a result of rotation about their vertical axes (Cooper and Poole, 1973). This is not the case with F18010. On this specimen the posterior five acrodont teeth tightly abut. The distal edge of each tooth is notched into the mesial edge of the posteriorly adjacent tooth. We have not seen this character in any other agamid.

DISCUSSION

Although anteriorly F18010 shows some similarity (a broad palatal process and the form of the acrodont teeth) to fossils assigned to the extant genus, *Physignathus* in this study, posteriorly the differences from *Physignathus* are marked. The tightly abutting posterior acrodont teeth are unique, and this state is not found in any other genera of Australian agamids examined. Even in genera where tooth wear plays an important role in shaping the posterior acrodont teeth (e.g. *Pogona*, *Chlamydosaurus* and *Physignathus*), the teeth remain broadly triangular in profile, rather than nearly quadrate as in F18010.

REFERRED SPECIMEN

QM F18015, fragment of right maxilla with four acrodont teeth (Fig. 11).

LOCALITY

?

DESCRIPTION

Fragment of right maxilla with four acrodont

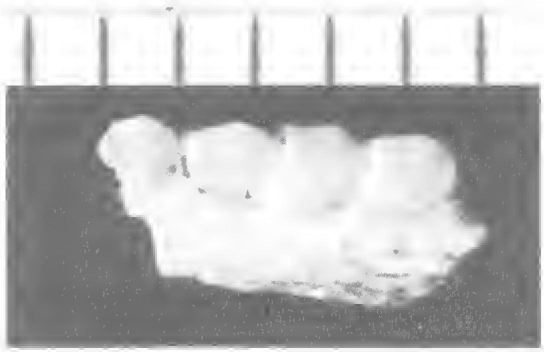
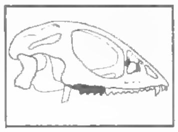


FIG. 11. *Sulcatidens quadratus* (QM F18015).

teeth. Maximum length 4.95mm; maximum depth (excluding teeth) 1.08mm.



In both labial and lingual view, no distinguishing features have been preserved on the maxilla. However, the acrodont teeth have a distinct chisel-like form. Viewed occlusally, the acrodont teeth are somewhat flattened on the labial face. The lingual face is gently rounded, and the teeth abut tightly. There is slight development of the 'tongue-in-groove' contact of the teeth seen in QM F18010.

DISCUSSION

F18015 shares with F18010 similar form of the posterior maxillary dentition. In F18010, each of the posterior five teeth is notched into the adjoining tooth. This is evident in F18015, but less pronounced. It may be that F18015 preserves the more anterior of the teeth showing this feature, or it may have derived from a younger individual that had not yet developed the notching to the extent seen in F18010. F18015 is referred to *Sulcatidens quadratus* gen. et sp. nov. because it has the distinctive notching in the posterior five teeth.

Family AGAMIDAE Gray, 1827
Unidentified Material

QM F18005

LOCALITY

Camel Sputum Site (Camel Sputum local fauna).

DESCRIPTION

Portion of left dentary bearing 6 posterior acrodont teeth. The anterior tooth row is badly

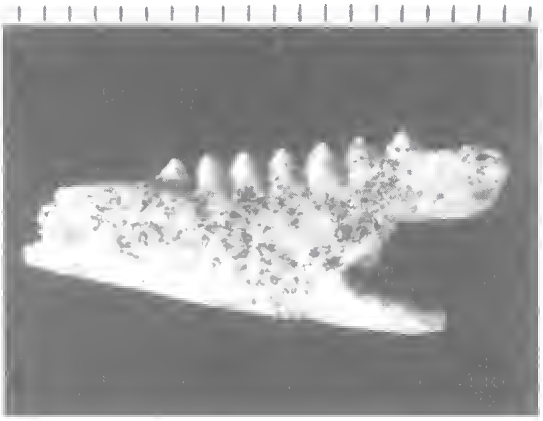


FIG. 12. Unidentified agamid (QM F18005).

worn so several acrodont teeth are missing. Length 19.75mm; maximum depth (excluding teeth) 7.40mm. The labial face of the dentary is badly eroded and it bears little surface detail (Fig. 12).

Posteriorly the acrodont teeth are weakly cusped, and there is deep vertical notching between the tooth bases labially. On the lingual surface a longitudinal groove, which shallows posteriorly, runs beneath the tooth bases. A large foramen is present in the roof of the Meckelian Groove below the acrodont tooth fourth from the posterior end. In occlusal view the tooth ridges are displaced towards the lingual surface.

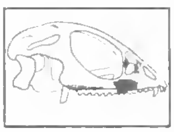
QM F18006

LOCALITY

Camel Sputum Site (Camel Sputum local fauna).

DESCRIPTION

A small fragment from the middle of the right maxilla. It bears two undamaged acrodont teeth and anteriorly the bases of three fragmentary acrodont teeth. Length 8.48mm; maximum depth (excluding teeth) 2.58mm.



On the labial face of the maxilla are three foramina, one below each of the broken acrodont teeth. The labial surface is curved in cross-section. On the lingual surface a groove runs above the acrodont tooth bases. The palatal process is broad. Viewed occlusally, the acrodont teeth have a flattened labial surface. The posterior acrodont tooth is very slightly tricuspid. Three foramina are present in a groove which parallels the maxilla/jugal/lacrimal suture medially. These foramina are tightly clustered, the posterior being the largest, and the anterior smallest.

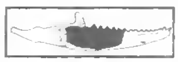
QM F18009

LOCALITY

Wayne's Wok (Wayne's Wok local fauna).

DESCRIPTION

Posterior fragment of right dentary, bearing one damaged and five complete acrodont teeth. Length 12.82mm; maximum depth (excluding teeth) 4.01mm.



Few distinguishing features are preserved on the labial surface. The posterior teeth are 'shouldered' and broadly triangular. Vertical notching is present at the tooth bases, except on the two posteriormost teeth. Viewed occlusally, both the lingual and labial tooth surfaces are well-rounded. The lingual surface of the dentary clearly displays a longitudinal groove running parallel to the tooth bases. At the posterior margin of the tooth row is a distinct depression in the surface, once carrying an additional acrodont tooth. The Meckelian Groove is clearly visible and contains a large foramen close to the anterior fracture.

QM F18011

LOCALITY

Wayne's Wok (Wayne's Wok site local fauna).

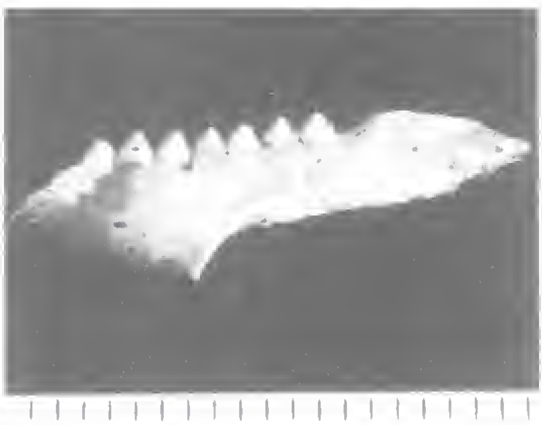


FIG. 13. Unidentified agamid (QM F18011).

DESCRIPTION

Damaged left dentary bearing seven acrodont teeth. The anterior one is damaged near the tip. Length 20.83mm, maximum depth (excluding teeth) 4.43mm. Viewed in labial aspect, the margin of the dentary/coronoid suture is well preserved (Fig. 13).

Two foramina are present on the labial face. One lies on the anterior fracture line. The other is immediately behind the damaged anterior acrodont tooth. Both foramina are displaced towards the ventral surface. The acrodont teeth are sharply pointed and inclined slightly back. The two hind-most teeth have a small cusp on the posterior edge. Deep vertical grooving is present between most of the tooth bases on the labial face of the dentary. However, the four posterior teeth do not show this. Viewed occlusally, the tooth ridge is slightly off-set labially and both tooth surfaces are gently rounded. The teeth curve slightly inwards, toward the lingual face. On the lingual surface of the dentary a well defined groove runs parallel to the tooth row, immediately below the tooth bases. A shallow cavity behind the posteriormost tooth has held a tooth. The damaged ventral surface of the dentary clearly exposes the Meckelian Groove in which there are two foramina, situated in the roof. The first and largest lies below the second acrodont tooth. The second is below the fourth acrodont tooth.

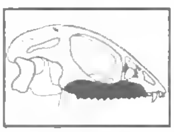
QM F18023

LOCALITY

Upper Site (Upper Site local fauna).

DESCRIPTION

Right maxilla bearing 12 acrodont teeth. Length 15.30mm, maximum depth (excluding teeth) 2.83mm. The posterior margin of the maxilla is well preserved.



Labially two foramina are present above the third and fifth acrodont teeth. Anteriorly a distinct ridge is present on the labial face, giving the lower labial surface a distinct inward curve. The acrodont teeth are not cusped and the tooth tips are well rounded. The two posteriormost teeth have a broader profile than the rest of the tooth row. Occlusally, most of the acrodont teeth are flattened on the labial face, and well rounded on the lingual face. The posteriormost tooth differs in being gently rounded on both faces and almost chisel-shaped with a distinct ridge at its tip. The second posteriormost tooth, although similar, has a flattened anterior face, giving the tooth three faces. The lingual face of the maxilla has a deep vertical notch along the tooth bases. A distinct groove runs parallel to the tooth row terminating before the posterior two acrodont teeth. The palatal process is widest towards the middle of the tooth row. From this point it slopes back towards the tooth row and reaches its narrowest point level with the fourth posteriormost acrodont tooth. From here, it broadens to form a distinct posterior flange level with the end of the acrodont tooth row. Above the palatal process is a deep groove at the base of the nasal process. This groove contains two closely-spaced, large foramina, which are situated above the fifth and sixth acrodont teeth.

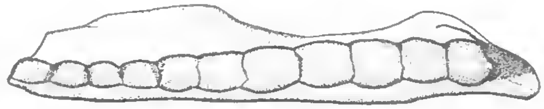


FIG. 14. Occlusal view of QM F18031 x3.

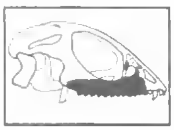
QM F18031

LOCALITY

Gag Site (Dwornamor local fauna).

DESCRIPTION

Right maxilla bearing 11 acrodont teeth (Fig. 14). Length 13.97mm; maximum depth (excluding teeth) 3.60mm. Labially three foramina are present, situated above the second, fourth and



fifth acrodont teeth. The teeth are broadly triangular, and cusped particularly on the posterior edge. Occlusally for most of the tooth row the labial face is flattened and the lingual face well rounded. The three posterior acrodont teeth are gently rounded on both faces. Their broad form and pronounced central ridge, give an almost chisel-like appearance. The lingual face of the dentary shows broad vertical grooving at the tooth bases, each groove located between adjacent teeth. As in fossil QM F18023 the palatal process is widest towards the middle of the tooth row. This tapers and then gives rise to a small posterior medial flange, level with the end of the tooth row. A deep groove at the base of the nasal process, contains three foramina, situated above the fourth and sixth acrodont teeth.

QM F18032

LOCALITY

Gag Site (Dwornamor local fauna).

DESCRIPTION

Left dentary fragment bearing three posterior acrodont teeth and a fragment of a fourth. Length 5.02mm; maximum depth (excluding teeth)

1.25mm. The only distinguishing feature on this fragment is the nature of the acrodont teeth. These are broadly triangular and tricuspid. Both the lingual and labial surface of the acrodont teeth are rounded when viewed occlusally. The tooth margin is displaced slightly toward the labial side. Slight rotation of the vertical axes gives the acrodont teeth some degree of overlap.

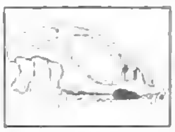
QM F18033

LOCALITY

Gag Site (Dwornamor local fauna).

DESCRIPTION

Right maxillary fragment bearing four acrodont teeth, probably originating from the



mid-posterior maxilla. Length 4.66mm; maximum depth (excluding teeth) 2.15mm. The only possibly distinguishing feature is one foramen on the labial surface. The teeth are broadly triangular and one is slightly shouldered. Viewed occlusally the teeth have a flattened labial face.

IDENTIFICATION

The specimens F18005-6, F18009, F18011, F18023, F18031-3 can easily be assigned to the Agamidae. All have fixed acrodont teeth, a major character of the family. However, the specimens are generally small and have worn or damaged teeth, or are otherwise damaged. They thus lack other characters useful in identification. One specimen (F18032) has distinctly triangular, tricuspid teeth. This is seen in *Physignathus*, *Chelosania*, *Caimanops*, *Gonocephalus*, and *Diporiphora* but, as no other useful characters are preserved on the specimen, it is impossible to refine its identification.

THE FAMILY AGAMIDAE, EXTINCT AND EXTANT

Fossil agamids are known from China, Mongolia, the Middle East, Belgium, France, southeastern Europe (including Crete), northeastern Africa, Wyoming (USA) and Australia (Estes 1983b). The oldest material is from the Cretaceous of China and Mongolia. Many taxa have been described from this region (Estes, 1983a; Holman, 1981; Hou, 1976). Estes (1983a) has reviewed the fossil record and early distribution patterns of lizards and concluded that agamids originated in the Late Cretaceous in southern 'Eurasia', the area which conforms today with South-east Asia and India, including part of Australia. This view is supported by both early and recent reports of Cretaceous agamids from Mongolia and China. *Anhuisaurus hauinanensis*, *Tinosaurus doumuensis*, and *Agama sinensis* (all of Hou, 1976) are agamids from the Palaeocene of China. Agamids are not present in North America (Estes, 1964; Holman, 1981), South America, or Europe. And fossils of appropriate age in Africa are so poorly known that it is impossible to comment on the presence of the group in Africa. The remaining material is more recent, from the Eocene, or, like that from Palestine and Australia (excluding the Riversleigh material), from the Pleistocene. The Australian fossil record of agamids is extremely poor. Estes (1984) describes, briefly, 'an acrodont lizard (presumably an agamid) from localities in the Wipajiri Formation ... Etadunna Formation ... South Australia.' This Middle Miocene fragment presents the first evidence of a possible agamid presence here. There is a gap in the record (prior to the discovery of the Riversleigh deposits) until the Pliocene. Archer and Wade (1976) report an agamid lizard similar to some species of *Amphibolurus* and Estes (1983a,b) reports part of a skull of *Chlamydosaurus kingii*. The only other agamid material is from the Pleistocene (Bennett, 1876; Smith, 1976, 1982).

The occurrence of modern agamids reflects this fossil record. Agamids are strongly represented in both Asia and Australia, which are widely regarded as centres of diversity for the group. The group is most diverse at both specific and generic levels on the Indian subcontinent. Dragons occur in Africa, southern Europe, and some Pacific islands. Species from Africa and southern Europe are not numerous, and belong to genera from India or the Middle East.

In Australia, 60–70 species are probably present, although not all are yet described. There is general agreement about species boundaries, but no such accord in regard to generic definition and allocation. Thus, there are several recent proposals regarding generic divisions (e.g. Witten, 1982a; Cogger, et al., 1983; Storr, et al. 1983; Wilson and Knowles, 1988). Here, we follow Storr et al. (1983), and Wilson and Knowles (1988), with minor modification.

THE AUSTRALIAN LEPIDOSAUR FOSSIL RECORD

In order to provide a perspective on the agamids from Riversleigh, we briefly review the history of the lepidosaurs in Australia. Molnar (1982, 1984a,b, 1985) summarized what is known from the fossil record here. The earliest remains are a Triassic (c.240 my) specimen identified as *Kudnu mackinlayi*. (*Kadimakara australiensis*, previously regarded as the oldest Australian lepidosaur, is referred to the sister group of the archosaurs, Molnar, 1990). Estes (pers. comm.) notes further that this species is not a 'lizard' and that no Triassic forms have the squamate synapomorphies. Some lacertilian fragments are known from the Lower Cretaceous (100my) of Victoria and a mosasaur has been recorded from the Upper Cretaceous of Western Australia. None of these have descendants amongst our modern fauna. Molnar (1985) describes 'a yawning gap' in the record and notes elsewhere (1982), that the bulk of Australian fossil lepidosaur material is of Pleistocene age. The Pleistocene remains belong either to essentially modern taxa or to extinct, related fossil taxa (e.g. *Varanus* vs *Megalania*).

PRE-RIVERSLEIGH HYPOTHESES

Despite a scant fossil record, a plethora of theories about the evolution of agamids in Australia has emerged (Heatwole, 1987).

1. Harrison (1928) noted three elements in Australia's fauna: A. Autochthonian which 'must have had its origins at a time when Australia was in connection with other land masses...'; B. Euronotian, '... which has reached Australia from elsewhere, and undergone radiation ... a bone of contention for a long time ... derived chiefly from South America, by means of antarctic connections...'; C. Papuan, '... not well-named since it came from further afield than New Guinea, through which is merely passed....' From his discussion of the occurrence of 'The Agamidae' (pp. 378-380) it can reasonably be inferred that he regarded the group as having fundamentally Asian origins (i.e. forming part of his Papuan element).

2. Cogger (1961) suggested '... there were 4 agamid invasions of Australia beginning some time in the early to mid Tertiary, all of which entered Australia via New Guinea. The earliest invasion was by the ancestor of *Moloch horridus*, the second one arrived probably in the Pliocene and gave rise to the amphiboluroid radiation.... The final two, *Physignathus lesueurii* followed by *Gonocephalus* species are little differentiated from their New Guinea relatives and are probably of recent origin. These two are found only in the wet, forested part of eastern Australia, whereas the older elements are primarily adapted to semi-arid regions....' This approach has been reiterated by Cogger and Heatwole (1984).

3. Witten (1982a) observed two possible explanations for the occurrence of agamids in Australia. 'Either (a) the family evolved in Asia and has spread into Africa and Australia, or (b) the family evolved in Gondwanaland, part of which now makes up Australia, Africa and the Indian subcontinent....' He regards *Physignathus* as one of the Asian-derived agamids in Australia, 'a more recent Australian arrival than *Chelosania*...' i.e. more recent than 10-20mya when he suggested the first Asian-derived agamid species invaded.

4. Estes (1983a,b) has a world view of the agamid fossil record and has commented in detail on origin and early distributions of the family. He described a Middle-Late Jurassic (190-145my) '... more northern Gondwanan acrodont iguanian group (which) underwent vicariance as the Asia-Southeast Asia-Australia-India blocks separated from Africa ...' and resulted in the agamids (in Asia and Australia) and in the chameleonids (in Africa). He notes elsewhere (p. 392) the centre of origin for the agamids (along with geckos, skinks, and varanids) during the Early Cretaceous (i.e. about 120my) as 'the conjoined area' of what is today India, Australia and Southeast Asia. Tyler (1979) has also contributed to this interpretation.

5. Greer (1990) contends that '... agamids evolved initially on the northern landmass and entered the southern continents, including Australia, only relatively late in their history...'

MODERN *PHYSIGNATHUS* SPECIES

The affinities of the bulk of the agamid fossils from Riversleigh lie with the extant genus *Physignathus*, the water dragons. Three species of *Physignathus* are currently recognised - *P. lesueurii*, *P. cocincinus* and *P. mentager*.

P. lesueurii occurs in coastal Australia from southern Victoria (Gippsland) to northeastern Queensland (Cooktown area), and in Papua New Guinea (Wilson and Knowles, 1988; de Rooij, 1915). That many species are shared between Papua New Guinea and Australia is the well documented result of several recent land links that have favoured the exchange of both open and rain forest faunas (de Rooij, 1915; Tyler, 1972; Storr, 1964; Covacevich and Ingram, 1980; Kikkawa, et al., 1981; Covacevich and McDonald, in press). That *Physignathus lesueurii* should have colonised Papua New Guinea from Australia (or vice versa) sometime in the last 100,000 years is not a matter for comment, as such colonisations are entirely consistent with patterns for other taxa. However, the Australo-New Guinean distribution of *P. lesueurii* presents a paradox. It seems reasonable to suggest that a non-specialised, reptile which could colonise an area that is now two separate land masses, should be rather 'evenly' distributed throughout its range. Such is not the case. *P. lesueurii* is listed from only the Western and Gulf Provinces (Whitaker et al., 1982) and from the Arfak Mts of Irian Jaya (de Rooij, 1915). In Australia, it ranges from the banks of the Endeavour River, Cooktown, NEQ to Victoria, some 2500km. A distribution including New Guinea and most of coastal, eastern Australia, but excluding Cape York Peninsula north of Cooktown, is unique amongst the vertebrates. This appears anomalous in the light of the generalised habits of *P. lesueurii*, which occurs in a wide variety of riparian habitats and is a catholic feeder. There are two possible explanations. 1. *P. lesueurii* occurred, and has, become secondarily extinct, on Cape York Peninsula north of Cooktown. 2. *P. lesueurii* occurs only in Australia and 'P. lesueurii' from Papua New Guinea is in fact another taxon whose status and affinities are not known.

P. cocincinus occurs on mainland southeast Asia, in Indochina and Thailand (Boulenger, 1885; specimens in the Musée National d'-Histoire Naturelle, Paris). Very little has been written about this species since Boulenger's (1885) work.

As the affinities of the bulk of the fossil material lie with *Physignathus*, any attempt at interpretation of the data presented by the fossils makes desirable an assessment of the relationship between the modern Australo-New Guinean representative of the group (i.e. *P. lesueurii*) and the Asian *P. cocincinus*. However, assessment of the status of the New Guinean taxon is not possible because of the lack of accessible material.

Skulls of *P. cocincinus* (MNHN, two specimens Ag8, here termed Ag81 and Ag82) and of *P. lesueurii* (several specimens, see specimens examined) are available to us. *P. cocincinus* and *P. lesueurii* resemble each other in general skull form, form of cusps on the teeth, the labial aspect of the teeth, position and size of maxillary foramina, and numbers of both acrodont and pleurodont teeth. In both species the maxillae are inflexed just above the tooth row. There is no discernable groove at the maxillary-jugal-lacrimal suture. In both, also, there is a marked longitudinal groove shallowing posteriorly below the tooth row of the dentary, although the degree of grooving varies slightly from side to side in Ag82 and also between the two specimens.

They differ in size, but there is only slight difference in proportion.

The shape of the parietal and frontal bones is distinct. In *P. cocincinus* these bones are broadly flattened, while in *P. lesueurii* they are more gracile and the occipital processes of the parietal are narrower. The posterior maxillary process in Ag82 lies above the second last maxillary tooth, while in J47973 it is just posterior to the last maxillary tooth. Further, the snout profile of *P. cocincinus* is acute rather than 'Roman', almost truncate, like that of *P. lesueurii*.

Notwithstanding the differences, the skulls of *P. cocincinus* and *P. lesueurii* are closer to each other than either is to skulls of any of the other genera examined by us or illustrated by Cooper, Poole and Lawson (1970). Skull sizes, shapes, and dentition, particularly the pleurodont teeth, distinguish the genera. Table 2 summarizes the results of our examination and that by Cooper, Poole and Lawson (1970) of the skulls of a wide range of agamid genera. *Physignathus* (including *P. cocincinus*) has 15 or more pleurodont teeth in total, made up of a maximum of 6 on the maxillae, 6 on the dentaries and up to 5 on the premaxilla. The presence of 3 caniniform pleurodont teeth on each dentary and each maxilla sets *Physignathus* apart from all other Australian and Asian agamids examined for this study.

The three spirit syntypes of *P. cocincinus* (MNHN 2537, 1856, 2536) have been examined by one of us (RM). They have no external features which suggest separation at the generic level from *P. lesueurii*. Because the specimens

TABLE 2. Numbers and sizes of pleurodont teeth in selected agamid taxa.

Taxa	Pleurodont Teeth			
	Premaxilla * Maxillaries	Dentaries *	Total Number	Size#
Physignathus lesueurii (QM specimens)	9–11	6	15–17	medium
+ *Physignathus lesueurii*	?	?	15	?
Physignathus cocincinus	10	6	16	medium
+ *Agama*	?	?	9, 9<15	?
Amphibolurus	5	3	8	large
Caimanops	8	4	12	large
+ *Calotes*	?	?	9 <15	?
Chelosania	7	4	11	small
Chlamydosaurus	3-7	0–3	3–10	large
Ctenophorus	7	4	11	medium
Diporiphora	3	3	6	large
+ *Draco*	?	?	9<15	?
Lophognathus	8	4	12	large
Hypsilurus	4–5	0	4–5	small
+ *Japalura*	?	?	9<15	?
+ *Liolepis*	?	?	9<15	?
Moloch	7	3	10	small
+ *Phrynocephalus*	?	?	9<15	?
Pogona	4–8	0–4	4–11	small
* *Uromastix*	?	?	9< 15	large

* based on actual teeth . # of largest teeth. + after Cooper, Poole and Lawson,(1970).

are old and faded, colour and pattern can not be assessed confidently. However, Taylor and Elbel (1958) describe distinct banding on the tail of *P. cocincinus* specimens from Thailand. Tails of *P. lesueurii* are also distinctly banded. Differences in size, degree of nuchal cresting, colour pattern, and head scalation, along with skeletal differences, warrant maintenance of the two species.

The status of *Physignathus mentager* Günther 1861 remains unresolved, but is inconsequential in a study of the Miocene *Physignathus* and their broad relationships. It was described by Boulenger (1885) from 'Siam' (= Thailand). Information on this taxon is scant, but comparisons between descriptions of *P. cocincinus* and of *P. mentager* suggest the latter could be a junior synonym of *P. cocincinus*. The authors of recent reviews of the reptiles of southeast Asia have not used the name *P. mentager*.

GENERA SHARED BETWEEN AUSTRALIA AND MAINLAND SOUTHEAST ASIA

Affinities between the faunas and floras of south-east Asia (including the archipelagos), Australia and New Guinea have long been the subject of observation and discussion. Among the modern lizard genera there is an easily demonstrated affinity. The following genera occur in both Australia and south-east Asia: *Cyrtodactylus, Hemidactylus, Gehyra, Lepidodactylus, Gonocephalus, Physignathus, Cryptoblepharus, Emoia, Sphenomorphus, Tropidophorus* and *Varanus*. It seems reasonable to suggest that this results from a combination of past continetal connections and recent migrations, either across the sea, or via land bridges at times of lowered sea levels. (New Guinea and the islands between it, and the Indonesian archipelago, abound with endemic genera which complicate the clear pattern evident at the Australia-Southeast Asian poles of the continuum of the Australasian region).

Notwithstanding the fact that close examination of the taxa shared between Australia and South-east Asia will undoubtedly bring about new allocations, and the recognition of new species and generic definitions, there are strong associations between the two continents.

DISCUSSION

'... The Water Dragons are so conspicuous that it cannot be supposed that they have been overlooked. Since they are aquatic and freely enter the sea, their distribution becomes even more remarkable and beggars explanation...'

Harrison 1928, p. 380.

The following Miocene agamids are now known from Australia:

Physignathus sp. (QM F18004, 18007-8, 18012-14, 18016-22, 18024-30); *Sulcatidens quadratus* gen. et. sp. nov. (QM F18010 holotype; 18015); unidentified (QM F18005-6, 18009, 18011, 18023, 18031-33).

In assessing the significance of the Riversleigh agamid material, we know that:

1. *Physignathus* sp. was present in Australia in the Miocene. *Physignathus* remains dominate the sample which also includes a taxon quite distinct from any extant form, *Sulcatidens quadratus* gen. et. sp. nov. The Riversleigh material establishes that agamids have had a much longer history here than has generally been supposed. Agamids have been here for at least 15-20my and the *Physignathus* represented appear to have changed little in that time.

2. Australia was separated by water from lands to the north until the late Miocene. This has been illustrated by Archer et al. (1989) at 40, 30, and 10mya. Despite the controversy about the exact details of the timing of fracturing of the continents and fluctuating sea levels, it is apparent that sea separated Australia from the archipelago to its north throughout the Eocene, and Oligocene and into the late Miocene. Thus, any dragons moving between Southeast Asia and Australia would have required high salt tolerance.

3. *P. lesueurii* lives in large numbers on the banks of the Brisbane River where salinity is of the order of 20 parts per 1000. The dragons, although terrestrial, use the water as a refuge. They readily enter the water and are capable of spending long periods submerged. This suggests a level of salt tolerance unusual in other Australo/New Guinean lizards observed. (Covacevich, pers. obs.)

4. *Physignathus* species occur coastally in both Australia (*P. lesueurii*) and SE Asia (*P. cocincinus*), and in the intervening area, New Guinea. Comparison of *P. lesueurii* and *P. cocincinus* indicates a close phylogenetic relationship.

5. Modern Australian agamids can be placed in two groups. *Physignathus, Gonocephalus* and possibly *Chelosania* form one group. The remaining genera all have a reduced number of microchromosomes, lack lacrimal bones, and are

adapted to arid or semi-arid conditions (Witten, 1983). It is not certain that these both represent monophyletic groups.

This evidence can be used to support two hypotheses about the origins of agamids in Australia. Either they have evolved from Asian stock that entered Australia across the seas or via land bridges about 20mybp. (An obvious corollary of this hypothosis is that they may have originated in Australia and colonized Asia), or the agamids had earlier origins in Gondwanaland. They are, today, conspicuous in some of the the southern continents.

Witten (1982) surmised that *Physignathus* was Asian and that the first of the Asian-derived agamids 'arrived' in Australia between 10 and 20mybp. He postulated that *Chelosania* was the most likely direct descendant of such an invasion and that *Physignathus* appeared '... to be a more recent arrival....'

The evidence presented here, coupled with the well-documented, long history of the Agamidae (at least from the Cretaceous) in China and near regions, most strongly support the suggestion that *Physignathus* is Asian-derived and that *P. lesueurii* and *P. cocincinus* are the direct and similar descendants of the Asian ancestral *Physignathus*.

It seems reasonable to infer from the agamid remains identified, that the Riversleigh environment in the Miocene may have resembled (in climate and forest profile, at least) present day coastal Queensland. If present requirements for *Physignathus* are relevant the area must have been well-watered. As *Sulcatidens quadratus* gen. et. sp. nov. is based on an incomplete maxilla and appears to have no obvious close relationships to any modern agamid genus, it reveals nothing of the palaeoecology of Riversleigh. Lepidosaurs are poorly known from the Miocene in Australia. *Egernia*, *Tiliqua*, *Varanus*, *Ramphotyphlops*?, *Morelia* (= *Python*), and *Montypythonoides*, have been reported (Molnar, 1990). In addition, we here report *Physignathus* and *Sulcatidens* gen. nov. Six of these eight genera are represented in the modern fauna. The extinction of *Sulcatidens* and *Montypythonoides* does not conform to this pattern of general conservatism in the Australia lepidosaurs.

NOTED ADDED IN PRESS

Since the review work for this paper was completed, 38 further agamid jaw fragments have been extracted from the Riversleigh matrix. The specimens have been registered into the Queensland Museum reference collection (F18044-F18081). There are no taxa represented in these fragments that differ from those already identified. All compare well with the initial sample. These specimens do not, therefore, alter the conclusions already drawn.

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